

Scanning Electron Microscopy Observation on Early Ontogeny of the Flower of *Camellia japonica* L.

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SEM によるヤブツバキの花の初期発生の観察
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The early ontogeny of a flower of *Camellia japonica* was studied with SEM. The flower is born on the axil of the lowermost bud scale of the winter bud. The spiral initiation of perules takes place in early summer, and three carpels and a whorl of 11 to 13 stamens are followed to arise in the simultaneous sequence at the floral apex. The multistaminate androecium is further initiated in the centrifugal manner and three layers of stamen rings finally arise around the gynoecium. The gynoecium initiates as three separated mounds at the tip of the floral apex but in the later development they are united to form a syncarpous gynoecium.

Introduction

The ontogenetical sequence of androecium whether the initiation to be centrifugal or centripetal has been considered to be significant on the classification of Dilleniidae (Cronquist 1981). Payer (1857) made brief observation on flowers of *Visnea mocanera*, *Thea viridis*, *Goldonia lasianthus* and *Ternstroemia peduncularis*, and first showed the centrifugal initiation of the androecia in the Theaceae. Erbar (1986) studied the floral development of *Stewartia pseudocamellia* (Theaceae) and reported that the fascicles of androecial primordium were initiated in the spiral order, born epipetally in the five clusters and located oppositely to five petals. Likewise in this species the initiation of each stamen was reported to be centrifugal within each fascicle. On the other hand the excep-

tions were found in Theales (sensu Cronquist), and the androecium did not show centrifugal development in both Actinidiaceae (Heel 1987) and Ochnaceae (Pauzé and Sattler 1978).

The present study was dealt with genus *Camellia* and focused to provide further comprehensive ontogenetical data for better understanding of so called "Guttiferalean Complex" (Cronquist 1968).

Materials and methods

The young flower buds of *Camellia japonica* were collected in July to January 1985 through 1989. All the materials were cultivated at the Botanical Gardens, University of Tokyo. The dissected young flowers were killed and fixed in FAA (Sass 1958), dehydrated in an ethanol series followed by critical point drying in liquid carbon

dioxide. The individual floral primordia in varied developmental stages were mounted on stubs, coated with gold and observed on a Hitachi S-405 Scanning Electron Microscope. The electron micrographs were taken on Fuji-SS 6×7 sheet film.

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Observations

The flowers of *Camellia japonica* are subtended by the lowest bud scales of a vegetative winter bud born on either axil or terminal. A single flower per bud is common but two flowers may be born on a single axillary bud. At the base of a short peduncle, two smaller bracteoles are located at the right angle to the bract. The floral appendages are consisted of 8 to 13 greenish sepaloid perules, 5 to 7 petaloid perules, multistamine androecium and three carpelate gynoecium forming united ovary. At the anthesis the petaloid perules are slightly connated at the base. Stamens are fused basally and adnated to the base of inner perules.

The floral appendages are initiated in a spiral order and the inner five are the petaloid perules (P1-P5) whereas the outer ones are the sepaloid (P6 to P9 are only shown in Fig. 1). The perules being incepted in the helical sequence, the floral apex is reduced in size and androecium and gynoecium initiation is followed in the later development stage. The inner perules (P1-P5) are successively initiated in the spiral sequence on the irregular pentagonal floral apex along its rim and to be petaloid in nature in later development (Fig.

2).

Prior to the initiation of androecium and gynoecium, the floral apex becomes broadly concave (Fig. 3). After the innermost perule (P1 in Fig. 2) has been initiated the humps of stamen and carpel initials become visible in the central region of the concaved floral apex (Fig. 4). These stamens and carpels initiate simultaneously and the earliest stamen primordia arise in a whorl of about 11-13 humps surrounding three carpel primordia. Following the initiation of the inner staminal whorl, further androecium is successively produced in the centrifugal manner so that the polyandrous concentric whorls surround the gynoecium at maturation (Fig. 5, 6).

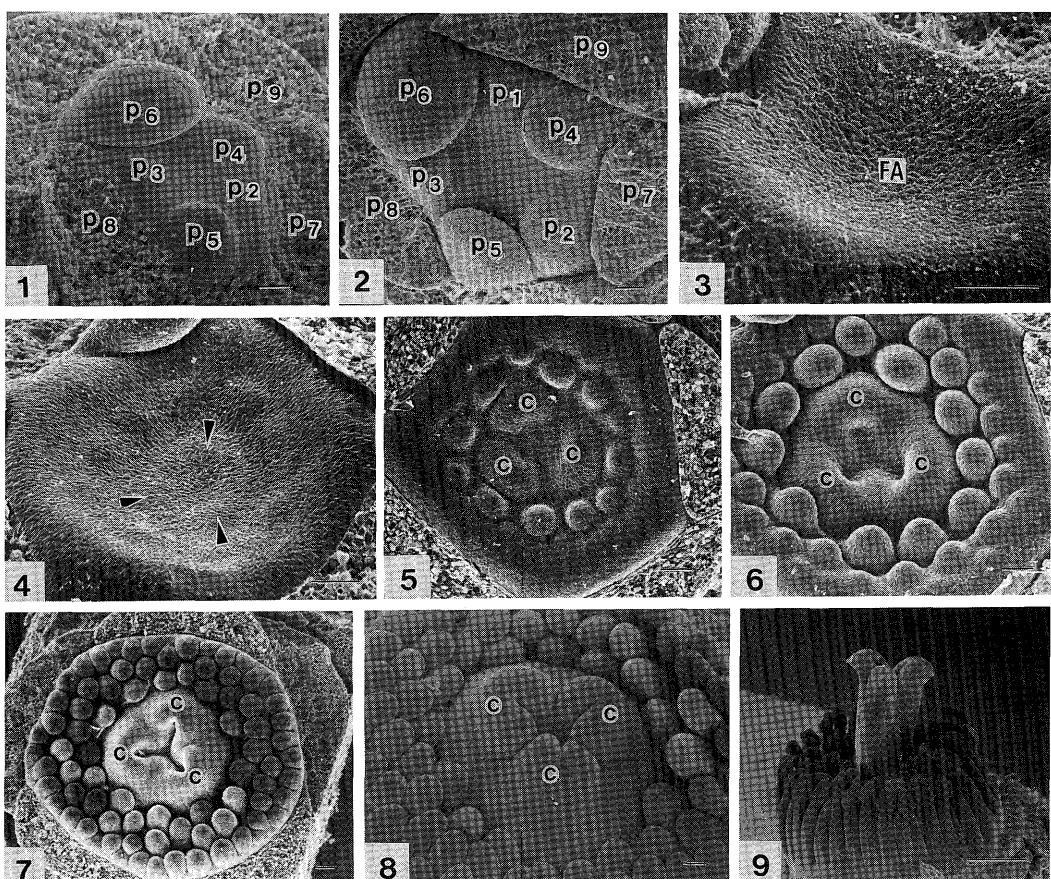
Three carpel primordia elongate longitudinally as a result of intercalary growth and each remains still independent at this developmental stage (Fig. 8). Later the carpel primordia become united at the base but remain free to the tips. The basal margins of the individual carpels are curved inward to form septa separating the locules (Fig. 8). When the flower is matured the syncarpous gynoecium has three free stigmata (Fig. 9).

In the mature flower of *C. japonica* the androecium is obviously epipetalous, however, multistamens are not initiated on the inner perules but directly incepted on the floral apex in the early stage of development.

Discussion

The current study is a part of detailed observations on the flower of the genus *Camellia* to report the early ontogeny of floral appendage and further paper on the floral vascularization will be forthcoming.

The flower of so-called "Guttiferaean Complex" (Cronquist 1965) is characterized to have a centrifugal androecium and a tendency to be stamen fascicles (Cronquist 1981). Although both



Figs. 1-9. SEM observation on ontogeny and development of the flower of *Camellia japonica*. 1-2: Perule initiation. 1. Petaloid perules are initiated but the innermost one (P1) is not yet appeared. Collected in July. 2. Five petaloid perules (P1-P5) are incepted forming a pentagonal rim around the floral apex. Collected in July. 3. Concaved floral apex showing no sign of the androecium nor gynoecium initiation at this stage. Collected in July. 4-9: Inception of androecium and gynoecium. 4. Both initiations take place simultaneously showing the androecium in a external ring and the gynoecium inside. The arrow heads indicate the independent carpel initiation. Collected in July. 5. Independent development of the gynoecium. Collected in July. 6. The androecium is initiated and developed centrifugally. The bases of three carpels are marginally united to form a syncarpic gynoecium. Collected in August. 7. Three whorls of the stamen ring are formed after the centrifugal initiation of androecium. Collected in August. 8. The upper part of each carpel elongates to differentiate free styles. Collected in September. 9. Each stamen is differentiated into the anther and filament while styles remain free on the gynoecium. Collected in November. P1-P9: Perules. The smaller figures for petaloid and the larger for separoid. FA: Floral apex. C: Carpel. Scale bars are 5 μ m for Figs. 1-8, and 50 μ m for Fig. 9.

“Woody Ranalean complex” and Rosidae have polyandrous flower the current taxon has been clearly set off from these two taxa in this respect. The Woody Ranalean Complex had the spiral androecium and Rosidae the centripetal.

The androecial initiation has been drawn the primary interest for those previous students and

earlier studies on the Guttiferalean Complex were much devoted to this point. Payer (1857) was the first to describe a centrifugal androecium in genera of *Thea*, *Visnea* and *Gordonia*, whereas Corner (1946) was first to point out the phylogenetical significance on the centrifugal development. Erbar (1986) studied floral ontogeny of *Stewartia*

pseudocamellia in the Theaceae and showed that 5 bulges of stamen fascicle primordia initiated in the spiral order opposite to 5 petals but individual stamens arose on each stamen fascicle primordium in the centrifugal sequence, which supported the phylogenetical value in the stamen development to the systematics (Erbar 1988).

Unlike *S. pseudocamellia* the stamen primordia of *C. japonica* are initiated first in a ring on the concaved floral apex not forming stamen fascicles (Fig. 5). The manner of androecial ontogeny was well agreed to Payer's earlier observation on *Thea* and *Gordonia*. In the later development of *C. japonica* the concentric androecial rings are laid centrifugally on the concaved floral apex so as to form a few layers of concentric multistaminate whorls surrounding the carpel initials (Figs. 7–9).

Eyde (1975) has summarized floral anatomy on the bases of angiosperm phylogeny and reviewed Leins' proposal (1971) for the scheme of androecium phylogeny. Leins speculated that the centripetal androecium occurred with convexed floral meristem and the centrifugal with concaved. The floral apex in *C. japonica*, however, is concaved but not convex as Leins had envisioned the evolutional lines on polyandrous dicotyledons. Although Leins' proposal is suggestive, it is not appropriate to discuss phylogeny with the current limited information. Although Erbar (1986) has suggested the complex centrifugal androecia to be archaic, further study would be needed for the phylogenetical evaluation whether the concentric ring of polymerous stamens advanced, or the fasciculate spiral archaic.

The other families in Theales were studied on the floral development of particular interest on stamen initiation. Heel (1987) studied the floral development of the Actinidiaceae and elucidated that in *Actinidia chinensis* stamen primordia were incepted as a single androecial whorl then each

primordium was subdivided to give rise to secondary stamen primordia in a centrifugal way and showed the concentric whorls of androecia. Pauzé and Sattler (1987) studied and depicted centripetal initiation of androecium in the Ochnaceae.

The ontogeny of the perianth member (perule) in the genus *Camellia* showed the spiral sequence and result was well agreed with Erbar's observation, she (1986) also reported the epipetalous stamen fascicle in *S. pseudocamellia*. The present species shows a similar flower structure at the anthesis that the androecium attached at the base of the connate inner perules. In *C. japonica* the epipetalous stamen could be a secondary phenomenon as a result of the multistaminate condition and of the spatial problem between the gynoecium and the rim of inner perules. The centrifugal stamen is a conversion of developmental sequence from acropetal to basipetal, and it may be caused by the spatial limitation for multistamens on the narrow concaved floral axis. There is a drastic discontinuity in the ontogeny of floral apex, and perules being developed in the spiral acropetal sequence but the androecium in the whorled and centrifugal (Figs. 1–2, 5–6). Our present knowledge is insufficient for near related taxa and extensive studies would be necessary for better understanding on this problem.

The gynoecial development is started with three separate bulges in the center of the concaved floral apex in *C. japonica* (Fig. 4). Their initiation takes place simultaneously with that of the innermost androecial whorl. The three individual carpels are later formed into a syncarpic gynoecium.

Much has been written on the centrifugal stamen development in Dilleniales and its allied taxa. Recent study in the Actinidiaceae (Heel 1987), and in the Ochnaceae (Pauzé and Sattler 1978) have opposed to the centrifugal stamen develop-

ment as not always being a reliable criterion for characterizing the Dilleniidae. The vascular anatomy of the flower and independent initiation of syncarpic gynoecium may provide better understanding of the families in Dilleniidae.

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要 旨

ヤブツバキの花の器官発生の初期を観察した。花被は14–19個が数えられるが、このなかの内側の5個（時には6個）は花弁性の花被とみなすことができる。これら内花被と外花被は連続したラセン配列を示す（Fig. 2）。内花被の分化が完了する時期になると花茎頂端が凹面状になる（Fig. 3）。まもなく雄蕊群と雌蕊群がほぼ同時期に原基を始原する。雌蕊は3個の独立した原基として発生し、これを取り囲んで環状にまず一重の雄蕊の原基11–13個を生じる（Fig. 4）。更に雄蕊は外側に向って同心円状に原基を発生し、明かに遠心的順序で発生を行い、ついに三重の環となる（Fig. 5, 6, 7）。雌蕊は独立した原基が発達し、やがてその基部の隣接するへりが同系合着して合生心皮を形成する（Fig. 6）が、花柱は離生したまま発達する（Fig. 9）。